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TESTING SPECIES BOUNDARIES WITHIN THE *ATRACTUS OCCIPITOALBUS* COMPLEX (SERPENTES: DIPSADIDAE)

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ABSTRACT: The taxonomic status of *Atractus occipitoalbus* is revised on the basis of concordance between quantitative and qualitative analyses of morphological characters (meristic, morphometric, color pattern, and hemipenis). *Atractus duboisi* and *A. orcesi* are herein resurrected based on the number of ventral and subcaudal scales, number of postocular scales, head shape in lateral view, relative tail length, distinct color patterns, and hemipenial morphology. Additionally, a new species, closely related to *A. occipitoalbus*, is described from the Andean piedmont of Colombia. The new species, represented by a single female, is diagnosed from the *A. occipitoalbus* female populations on the basis of number of subcaudals, number postocular scales, and dorsal and ventral color patterns.

Key words: *Atractus duboisi*; *Atractus occipitoalbus*; *Atractus orcesi*; Geographical variation; Species boundaries; Taxonomy

THE CRYPTOZOIC snake genus *Atractus* Wagler is distributed widely in the Neotropical region, occurring from Panama to Argentina (Giraudo and Scrocchi, 2000; Myers, 2003). *Atractus* is the most specious Alethinophidian snake genus, having currently 125 valid species, most of them known only from their type localities (Passos, 2008). Despite of many recent works focusing on this genus (Hoogmoed and Prudente, 2003; Jorge da Silva et al., 2005; Kok, 2006; Markezich and Barrio-Amorós, 2004; Myers, 2003; Myers and Schargel, 2006; Passos and Arredondo, 2009; Passos and Fernandes, 2008; Passos et al., 2005; Passos et al., 2007*a*,*b*; Schargel and Castoe, 2003; Schargel and Garcia-Pérez, 2002; Zaher et al., 2005), additional efforts must be made to address problems of morphological variation, geographic ranges, sexual dichromatism, and ontogenetic change of coloration for most *Atractus* species (Passos et al., 2009*a*,*b*). Consequently, only with the study of all of these aspects we can shed more lightly on the species delimitation of this complex and poorly known genus (Passos, 2008).

Rhabdosoma occipitoalbum Jan was described based on a single specimen from the Andes of Ecuador without a more specific locality, and the holotype picture was provided by Jan and Sordelli (1865). Similarly, Boulenger (1880) described *R. duboisi* based on a single specimen from an unknown locality in the Andes of Ecuador. Subsequently, Boulenger (1894) synonymized the genus *Rhabdosoma* Günther (= *Rabdosoma* Duméril & Bibron) with *Atractus*, recognizing *Atractus occipitoalbus* and *Atractus duboisi* as valid species. Savage (1955) described *Atractus orcesi* from Loreto, Province of Pastaza (currently Province of Orellana), on the Amazon versant of the Andes of Ecuador distinguishing this taxon from *A. occipitoalbus* based on the number of maxillary teeth, ventrals, and supralabials in contact with the orbit (Savage, 1955, op. cit.). Later, Savage (1960) synonymized *A. duboisi* and *A. orcesi* with *A. occipitoalbus* mainly due to the large overlap in the scale counts and difficulties in the interpretation of the variation in color pattern.

In this paper we evaluate the taxonomic status of the currently recognized *Atractus occipitoalbus* (sensu Savage, 1960) on the basis of concordance between qualitative and quantitative analyses of morphological characters.

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Materials and Methods

Material and Techniques

Institutional abbreviations follow Leviton et al. (1985), except for the following institutions that had acronym alterations or were not included in these sources: UK—Natural History Museum (NHM), London. Colombia—Colección Herpetologica de la Universidad de Quíndio (UQC), Armenia, Quíndio; Instituto Alexander Von Humboldt (IAvH), Villa de Leyva, Boyacá; Instituto de Ciencias Naturales (ICN), Universidad Nacional de Colombia, Bogotá, D.C.; Museo de Zoología de la Universidad Javeriana (MUJ), Bogotá, D.C. Venezuela—Museo de Historia Natural de la Fundación La Salle (MHNFL), Caracas, D.C.; Laboratorio de Biogeografia de la Universidad de los Andes (ULABG), Mérida, Mérida; Museo de Biología de la Universidad de Los Andes (CV-ULA), Mérida, Mérida. Brazil—Coleções Herpetológicas do Museu da Universidade Estadual de Feira de Santana (MZUEFS), Feira de Santana, Bahia; Instituto Butantan (IBSP), São Paulo, SP; Museu Zoológico Augusto Ruschi, Universidade de Passo Fundo (CRUPF), Passo Fundo, RS. Ecuador—Museo de Zoología, Pontificia Universidad Católica del Ecuador (QCAZ), Quito. Peru—Museo de la Universidad Mayor de San Marcos (MHNSM), Lima, Peru. Bolivia—Colección Boliviana de Fauna (CBF), La Paz; Museo Noel Kempff Mercado (MNKR), Santa Cruz de La Sierra, Bolivia. Argentina—Universidad Nacional del Nordeste (UNNEC), Corrientes. All specimens examined having 15 dorsal scale rows were listed in the Appendix I.

Terminology for *Atractus* cephalic shields follows Savage (1960), and the method of counting ventral scales follows Dowling (1951). Techniques for hemipenis preparation follow Pesantes (1994). Terminology for hemipenis description follows Dowling and Savage (1960) as augmented by Myers and Campbell (1981) and Zaher (1999). We determined sex by subcaudal incision. Measurements were taken with an analogical caliper to the nearest 0.1 mm under stereoscope, except for snout–vent (SVL) and caudal lengths (CL), which were taken with a flexible ruler to the nearest 1 mm.

Species Concept and Diagnosis Criteria

In this study, we followed the general lineage species concept according De Queiroz (1998). We consider the presence of one or more exclusive, apparently fixed diagnostic character, which distinguishes a given taxon from the others in the *A. occipitoalbus* complex, as species delimitation criteria. Nonetheless, as the sample size accessed here did not allow access the statistical confidence from qualitative characters for some populations (sensu Wiens and Servedio, 2000), we alternatively look for concordance between the discrete and continuous characters. Since these features are likely uncorrelated, the correspondence between these kinds of data might represent independent evidence of species boundaries (see Passos and Fernandes, 2009, for discussion on the use of the concordance approach for discrete and continuous characters).

Statistical Analyses

We partitioned our sample into three groups on the basis of distinct color patterns and hemipenis morphologies to evaluate quantitative differentiation within *Atractus occipitoalbus* (sensu Savage, 1960). Group 1 included specimens with a dorsal color pattern of paired yellowish blotches on a dark background, a wide midventral stripe, and semicapitate and semicalyculate hemipenis. Group 2 included specimens with a uniform black dorsal background except for light occipital transverse band, uniformly black venter, and non-capitate and slightly semicalyculate hemipenis. Group 3 included specimens with a dorsal color pattern having vertebral and dorsolateral longitudinal stripes, a wide midventral stripe, and non-capitate and semicalyculate hemipenis.

We employed an Analysis of Variance (ANOVA) to assess the presence or absence of sexual dimorphism within the whole sample, and also for evaluate group differentiations. We evaluated the assumptions of univariate normality by inspection of the normality plots and homocedasticity through Levene test (Zar, 1999). In cases where characters showed insufficient variation to justify these assumptions, we performed non-parametric tests such as Mann-Whitney

and Kruskal-Wallis (Zar, 1999). We performed a Discriminant Function Analysis (DFA) at group level to evaluate the quantitative discrimination between the groups diagnosed previously on the basis of discrete differences (e.g., color pattern and hemipenis morphology). We projected the first two discriminant functions onto orthogonal axes and computed 95% confidence regions from the simulation of 1000 pseudoreplicate data matrices obtained by parametric bootstrap (Efron, 1979; Manly, 2000). Classification matrices based on DFA scores were produced to determine how well individuals could be allocated into their correct populations (Passos and Fernandes, 2009; Rossman and Burbrink, 2005). All discriminant function loadings were portrayed as vector correlations (directional cosines), which were estimated for each variable by correlations with projection scores across individuals (Wright, 1954). This procedure reveal the original variable closely correlated with the discriminant functions (Strauss, 1985). We estimated the missing values through the *missing* function in MATLAB software. Individuals or variables with missing data above 30% were not considered in the statistical analyses.

We used the following variables in the statistical analyses: number of ventral scales (VENT), number of subcaudal scales (SUBC), number of dorsal scales in the level of second subcaudal (DORT), number of supralabial scales (SUPR), number of infralabial scales (INFR), number of infralabials contacting chinshields (CHIN), number of gular scales (GULA), number of preventrals (PREV), number of postocular scales (POST), number of maxillary teeth (TEET), and SVL/CL ratio (SVLT). We performed all analyses using the software STATISTICA 5.0 (StatSoft, 1998), except for missing values estimatives, discriminant analysis, bootstrap, and plot of directional cosines for which we used MATLAB 4.2c1 (MathWorks, 1994).

Results

Although all variables employed in the statistical analyses displayed comparable variances for each defined group, some of them did not have normal distributions into the groups. For that reason, we used those variables only in the DFA with bootstrap confidence intervals (Passos and Fernandes, 2009). Groups showed significant sexual dimorphism in the number of ventral ($F_{67,7} = 43.1$, $P < 0.001$, $n = 115$) and subcaudal scales ($F_{12,2} = 564.5$, $P < 0.001$, $n = 115$), as well as SVL/CL ratio ($F_{4,8} = 395.9$, $P < 0.001$, $n = 101$). Therefore, these characters were treated separately for each sex in all subsequent analyses. Group comparisons showed significant differences for females in the number of ventral scales ($H = 52.8$, $P < 0.001$, $n = 94$), subcaudal scales ($H = 53.0$, $P < 0.001$, $n = 93$), postocular scales ($H = 81.1$, $P < 0.001$, $n = 94$), and SVL/CL ratio ($H = 49.2$, $P < 0.001$, $n = 94$). Males showed differences in the number of ventral scales ($H = 47.2$, $P < 0.001$, $n = 70$), subcaudal scales ($H = 37.4$, $P < 0.001$, $n = 71$), and SVL/CL ratio ($H = 17.3$, $P < 0.001$, $n = 71$).

The projections of the bivariate plots based on the scores of discriminant analyses were able to discriminate three female groups (Fig. 1A), for which about 98% of individuals were correctly allocated through Jackknife classification (Table 1). First two discrimination functions correspond to 100% of the entire variation, and were strongly correlated with VENT, SUBC, SVLT, INFR, CHIN, and POST (Table 2). The DFA of females reveals that group 2 was distinguished from groups 1 and 3 mainly by first axis, which was correlated principally with INFR, POST, SBCD, and SVLT. On other hand, populations 1 and 3 were separated from each other by second discriminant function strongly correlated with VENT, CHIN, and GULA (Fig. 2A, Table 2).

Discriminant functions were unable to entirely separate males into a priori defined groups (Fig. 1B). Despite broad overlapping in the bivariate space between Group 3 and Groups 1 and 2, male populations attained values above 90% of correct allocation in the classificatory function of DFA (Table 3). Although the male's confidence ellipses overlapped among the groups, the centroid from Group 3 was located considerably outside the other two ellipses. Group 2 was distinguished from the other two mainly by the second discriminant function, which was strongly correlated with GULA, whereas, Groups 1

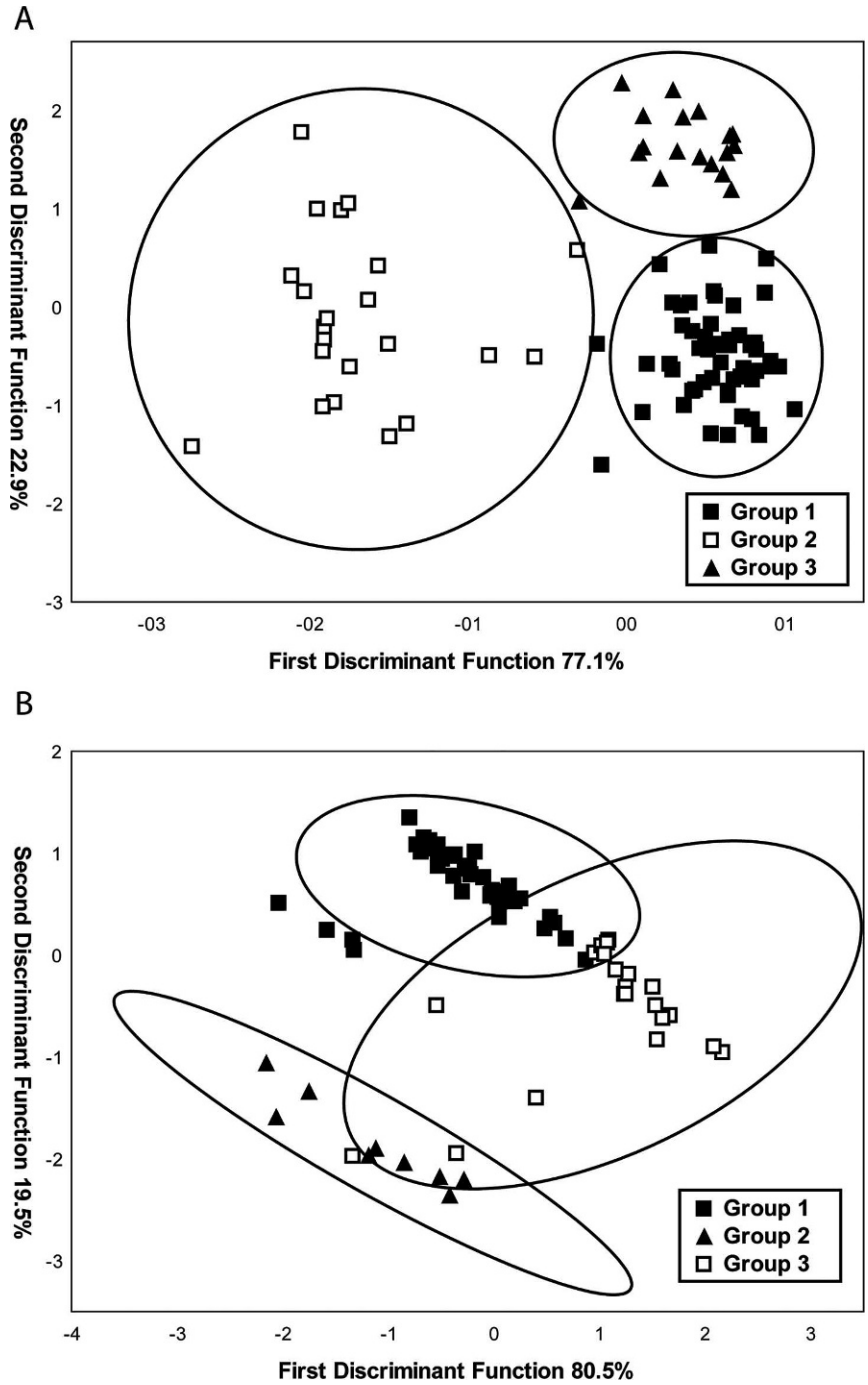

FIG. 1.—Bivariate plot with 95% confidence regions and 1000 bootstrap pseudoreplicates for the first 2 axes derived from scores of discriminant analysis for females (A) and males (B).

TABLE 1.—Classificatory matrix from discriminant analysis for three defined groups of females, showing individuals correctly allocated based on the classification by Jackknife.

Groups	Percentual of correct classification	1	2	3
1	100%	53	0	0
2	90.9%	1	20	1
3	100%	0	0	18
Total	97.8%	54	20	19

and 3 separate from each other by the first discriminant function, represented mainly by VENT and SVLT (Fig. 2B, Table. 4). Still, all variables strongly correlated with the first discriminant function were also heavily correlated with the second (Table. 4), making the second axis nearly redundant.

Regardless of partial overlapping with males, the morphometric analyses support recognition of three taxa in the eastern versant of the Andes of Colombia and Ecuador, which is largely paralleled by qualitative characters (e.g., coloration, head shape, and hemipenial morphology). Groups 1, 2, and 3 have coloration patterns very similar to those of the holotypes of *Atractus duboisi*, *A. occipitoalbus* (see Jan & Sordelli, 1865), and *A. orcesi* (see Savage, 1955), respectively. Based on the congruence results from the quantita-

TABLE 2.—Eigenvectors, eigenvalues, and percent variance explained for the first two axes of discriminant analysis of non-transformed data for three defined groups of females. Loadings in bold font correspond to the original variables heavily correlated with the respective discriminant functions.

Variable	DF I	DF II
VENT	−0.3921	**0.9202**
SUBC	0.0257	**−0.8025**
SVLT	**0.6092**	0.2410
DORT	−0.2129	0.1220
SUPR	0.1410	−0.3115
INFR	**0.8101**	0.3564
CHIN	**−0.7032**	−0.2559
GULA	0.1916	0.1161
PREV	0.0596	0.0766
POST	**−0.9274**	0.0007
Eigenvalues	7.509065	2.227686
Percent of variance	77.1	22.9

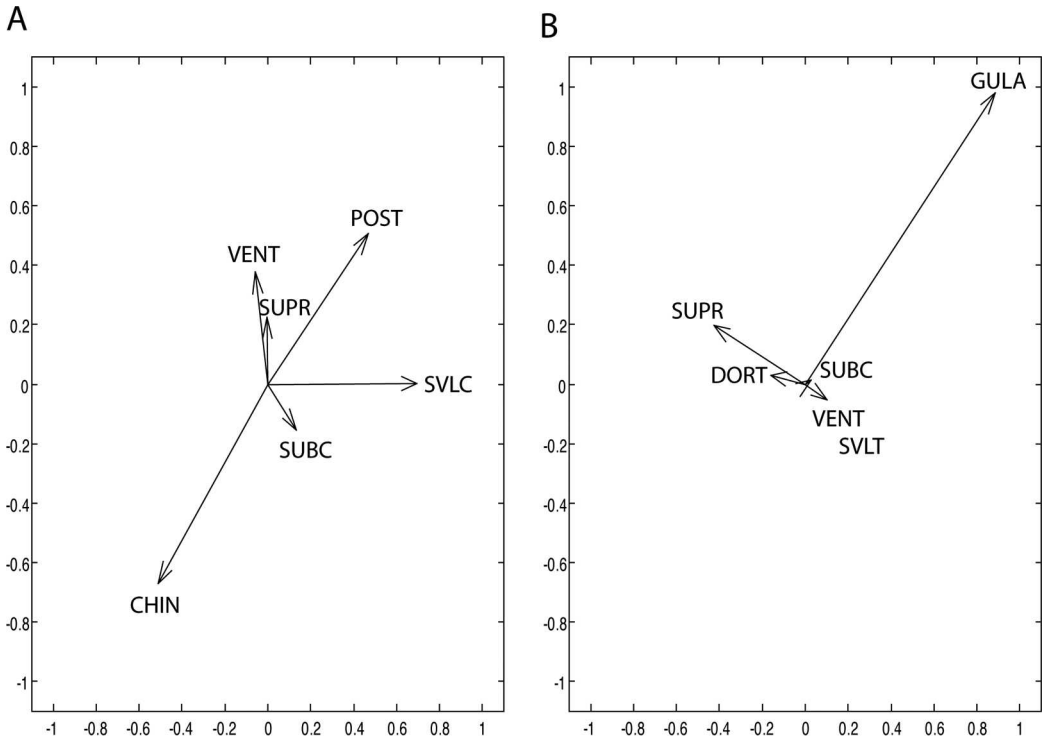

FIG. 2.—Simplified directional cosines showing the correlation vectors from original variables and loadings from female (A) and male (B) discriminant analysis. Overlapping small magnitude vectors were deleted from graph.

TABLE 3.—Classificatory matrix from discriminant analysis for three defined groups of males, showing individuals correctly allocated based on the classification by Jackknife.

Groups	Percentual of correct classification	1	2	3
1	95.2%	40	0	2
2	100%	0	9	0
3	90%	0	2	18
Total	94.5%	40	11	20

tive and qualitative characters we resurrect *Atractus duboisi* (Group 1) and *A. orcesi* (Group 3) from the synonymy of *A. occipitoalbus* (Group 2).

Besides, in the course of this study we found a single female from the locality of Paraiso in the Western Cordillera piedmont of Colombia that did not match to any recognized species of *Atractus*. This specimen is apparently closely related to *A. occipitoalbus* by shared exclusive discrete characters (e.g., dorsal color pattern of the head and dorsum), meristics (low number of subcaudals), and morphometrics (relatively small tail size). Therefore, we describe this individual as new a species allied to the *A. occipitoalbus* complex, and compare it in detail with *A. occipitoalbus*.

SPECIES ACCOUNTS

Atractus occipitoalbus *(Jan, 1862)*

Rhabdosoma occipitoalbum Jan, 1862; Archivio per la Zoologia l' Anatomia e Fisisologia 2:16.

Atractus occipitoalbus—Boulenger, 1894; Catalogue of the Snakes in the British Museum 2:310.

Atractus occipitoalbus—Savage, 1960; Miscellaneous Publications of the Museum of Zoology, University of Michigan 112:60 (part).

Holotype.—Adult female, originally housed at the Zoologische Saatssmmlung München (ZSM 1395), collected by M. Wagner in the "Andes of Ecuador" about 1200 m elevation. The holotype is lost (Franzen and Glaw, 2007).

Diagnosis.—*Atractus occipitoalbus* can be distinguished from all congeners by the combination of the following characters: (1) 15/15/15 dorsal scale rows smooth; (2) 2 postoculars in males and usually 1 in females; (3) loreal moderate; (4) temporals 1+2; (5) usually 8 supralabials, 4–5th contacting orbit; (6) generally 7 infralabials, first 4 in contact with chinshields; (7) 6–8 maxillary teeth; (8) generally 4 series of gular scales; (9) generally 4 preventrals; (10) 143–172 ventrals in females and 129–155 in males; (11) 9–17 subcaudals in females and 20–26 in males; (12) dorsal color pattern uniform black, with a light occipital band; (13) venter generally uniform black; (14) small size, females reaching 262 mm and males 197 mm SVL; (15) tail size small in females (4.4–6.9% SVL) and moderate (9.6–14.1% SVL) in males; (16) hemipenis moderately bilobed, non capitate, and slightly semicalyculate.

TABLE 4.—Eigenvectors, eigenvalues, and percent variance explained for the first two axes of discriminant analysis of non-transformed data for three defined groups of males. Loadings in bold font correspond to the original variables heavily correlated with the respective discriminant functions.

Variable	DF I	DF II
VENT	**0.5587**	**−0.5990**
SUBC	0.1719	0.1634
SVLC	**0.3676**	**−0.3649**
DORT	−0.1692	0.0603
SUPR	−0.3822	0.3401
GULA	**0.4090**	**0.8723**
Eigenvalues	4.264260	1.032459
Percent of variance	80.5	19.5

Comparisons.—Among all *Atractus* species with 15 dorsal scale rows, *Atractus occipitoalbus* shares 1 postocular in females specimens only with *A. carrioni*, *A. elaps*, and *A. roulei* but differs from these by having 7–8 supralabials and an uniform dark brown dorsum with a light (creamish white) band on the occipital region (vs. 6 supralabials and no light collar on occipital region). Additionally, it can be distinguished from other *Atractus* species with 15 dorsal scale rows having eventually a light occipital band (*A. albuquerquei*, *A. boettgeri*, *A. emmeli*, *A. reticulatus*, *A. paraguayensis*, and *A. taeniatus*) by having 7–8 supralabials (6 in *A. albuquerquei*, *A. boettgeri*, and *A. taeniatus*), 7 maxillary teeth (8–9 in *A. paraguayensis*), and 9–20 subcaudal scales in females (27–44 in *A. albuquerquei*, 27–43 in *A. boettgeri*, 22–30 in *A. emmeli*, 21–27 in *A. reticulatus*, 21–30 in *A. paraguayensis*).

Description.—Head lacking cervical constriction, flattened in lateral, subtriangular in

dorsal view, twice as long as wide; snout slightly acuminate in lateral, round in dorsal view; rostral sub-triangular, broader than high, barely visible from above; internasal as long as wide; internasal suture sinistral with respect to prefrontal suture; prefrontal longer than wide; supraocular sub-triangular, twice as long as wide; frontal triangular, longer than wide; parietal twice as long as wide; nasal divided; nostril located between prenasal and postnasal; prenasal about 3 times as high as long; postnasal as long as wide, similar in height to prenasal; loreal moderate, generally contacting 2–4th supralabial; pupil round; usually 1 postocular in females and 2 in males; postocular generally as long as high in females, and upper postocular twice as high as long in males; temporals 1+2; anterior temporal twice as long as high; upper posterior temporal elongate, 3–4 times as long as wide; generally 8 supralabials, 4–5th contacting orbit; 2nd and 3rd supralabials similar in size and higher than first supralabial; 4th supralabial higher than 2nd and 3rd ones; 6th supralabial higher and 8th longer than remaining supralabials; symphisial sub-triangular, twice as broad as long; generally 7 infralabials, first 4 in contact with chinshields; first pair of infralabials in contact behind symphisial; chinshields twice as long as wide; generally 4 preventrals; 15/15/15 dorsal scale rows; dorsals smooth, without apical pits, supranal tubercles, and keels; caudal spine with moderate length, robust, conical, and slightly acuminate; maxilla arched in dorsal view, with 5–6 prediastemal and 2 postdiastemal teeth; prediastemal teeth large, robust at the base and acuminate on the apices, angular in cross section, curved posteriorly; prediastemal teeth moderately spaced, and with equivalent size; maxillary diastema moderate; postdiastemal teeth half the size of prediastemal ones; lateral process of the maxilla little developed, lacking posterior projection.

Color pattern in preservative.—Dorsum of head black, except for a creamish-white large occipital band covering parietals; black-cap occasionally with diffuse small dark brown dots; black pigmentation sometimes overlaps anterior margin of parietals; head uniformly black between snout and postocular region; postocular scale and anterior portion of first temporal scale generally black pigmented; parietal, temporal and occipital regions generally immaculate creamish white; supralabials mostly black, except for 8th supralabial creamish white; occasionally ventral portion of 6–7th supralabials with irregular small light dots; light occipital band reaching first dorsal scale rows; mental region and preventrals immaculate creamish white; venter with first two or three ventral scales cream, and uniformly black posteriorly; sometimes, there is two weakly defined paraventral lines on the margins of ventral scales; subcaudals uniform black, sometimes having also narrow paraventral lines; dorsum of body uniform black (Fig. 3).

Hemipenis.—Inverted organ bifurcates at eight and extends to level of ninth subcaudal. Fully everted and almost maximally expanded hemipenis rendered a moderate bilobed, non capitate, and slightly semicalyculate organ; lobes uniformly covered with moderate curved spines; spines progressively replaced by papillae toward lobe apices; spines connected transversally constituting barely defined calyces; calyces lacking distinct vertical walls; each lobe slightly distinct rounded on the apical portion; lobes approximately the same size; sulcus spermaticus divides about half of organ; branches have centrifugal orientation terminating on the tip of the lobes; margin of sulcus spermaticus stout, bordered by series of spinules from the base of organ to the crotch of lobes; hemipenial body uniformly covered by medium-size hooked spines; basal naked pocket longer than wide located laterally on the basal portion of hemipenial body; naked pocket extending to mid portion of the hemipenial body; most basal portion of hemipenial body nude, except for some dispersed spinules (Fig. 4A).

Variation.—Largest male 197 mm SVL, 19 mm CL; largest female 262 mm SVL, 16 mm CL; tail 9.6–14.1% ($\bar{x}$ = 11.8, SD = 1.6, n = 9) of the SVL in males and 4.4–6.9% ($\bar{x}$ = 5.6, SD = 0.6, n = 19) of the SVL in females; ventrals 129–155 ($\bar{x}$ = 141, SD = 9.1, n = 9) in males, 143–172 ($\bar{x}$ = 157.1, SD = 8.2, n = 22) in females; subcaudals 20–26 ($\bar{x}$ = 22, SD = 2.3, n = 9) in males, 9–17 ($\bar{x}$ = 13.4, SD = 1.9, n = 22) in females; postoculars 2 (n = 20 sides) in males, 0 (n = 1 side), 1 (n = 12

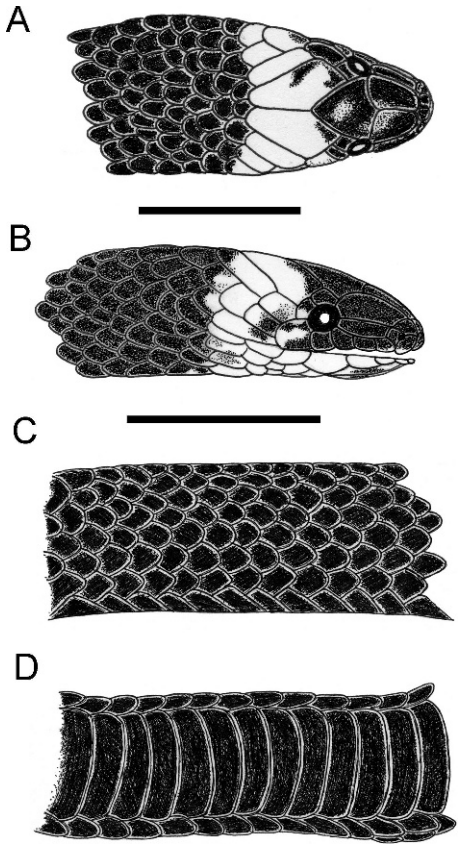

FIG. 3.—Dorsal (A) and lateral (B) views of the head, and dorsal (C) and ventral (D) views of the body of *Atractus occipitoalbus* (ICN 10116). (Scale = 5 mm.)

sides) or 2 (n = 4 sides) in females; 7 (n = 8 sides) or 8 (n = 52 sides) supralabiais; 7 (n = 58 sides) or 8 (n = 2 sides) infralabiais; 1–4 (n = 57 sides) or 1–5 (n = 3 sides) infralabials contacting chinshields; 3 (n = 4 sides) or 4 (n = 16 sides) gular scale rows; 4 (n = 10 sides) or 5 (n = 1 side) preventrals; 6–10 ($\bar{x}$ = 7.7, SD = 1, n = 22) dorsal scale rows of tail in the level of second subcaudal; 6 (n = 2 sides), 7 (n = 27 sides) or 8 (n = 1 side) maxillary teeth; retracted hemipenis extends to the level of 9th subcaudal (n = 2 sides).

Distribution.—*Atractus occipitoalbus* occurs in the Amazon versant of the Andes on eastern Ecuador and southeastern Colombia, from El Orito (04° 14′ N, 76° 52′ W) in the Putumayo Department of Colombia to Loreto (00° 40′ S 77° 19′ W) in the Orellana Province of Ecuador. This species inhabits Amazon plant formation or Gallery forest of the rivers from Andean piedmont and Amazon lowlands of Ecuador and Colombia, ranging from 300–1000 m. Although Carrillo and Icochea (1995) reported this species for Peru in the Departments of Cusco, Junín, and Ucayali, one of us (P. Passos) has examined the referred specimens from the MHNSM collection and concluded that they belong to a different taxon (Fig. 5).

Remarks.—The holotype of *Rhabdosoma occipitoalbum* was deposited in the ZSM collection and later was probably lost during the Second World War (Franzen and Glaw, 2007). Nonetheless, the original plate of Jan and Sordelli (1865) depicting the holotype permits the undoubted association of specimens having a uniformly black dorsal and ventral color pattern with a large light band on the occipital region and a single postocular (in females) with *Atractus occipitoalbus*.

Atractus duboisi *Boulenger, 1880* *(Status revalidated)*

Atractus duboisi Boulenger, 1880; Bulletin de la Société Zoologique de France 1880:44
Atractus occipitoalbus—Savage, 1960; Miscellaneous Publication of the Museum of Zoology, University of Michigam:60 (part).

Holotype.—Adult male, housed at Musée de l'Institut Royal des Sciences Naturelles de Belgique (RBINS 2008), from Ecuador, gift by Mr. De Ville in 1874, without specific locality (specimen photograph examined).

Diagnosis.—*Atractus duboisi* can be distinguished from all other congeners by the following combination of characters: (1) 15/15/15 dorsal scale rows, without apical pits, supranal tubercles, and kells; (2) 2 postoculars; (3) loreal long; (4) temporals 1+2; (5) generally 8 supralabials, with 4–5th contacting orbit; (6) generally 7 infralabials, first 4 in contact with genials; (7) 7 maxillary teeth; (8) usually 4 series of gular rows; (9) usually 4 preventrals; (10) 159–172 ventrals in females and 150–167 in males; (11) 13–21 subcaudals in females and 23–26 in males; (12) dorsal color pattern dark brown or black with a series of small, yellowish paired paravertebral dots; (13) venter with a creamish-white background and a wide, longitudinal, midventral black stripe; (14) moderate size, females reaching

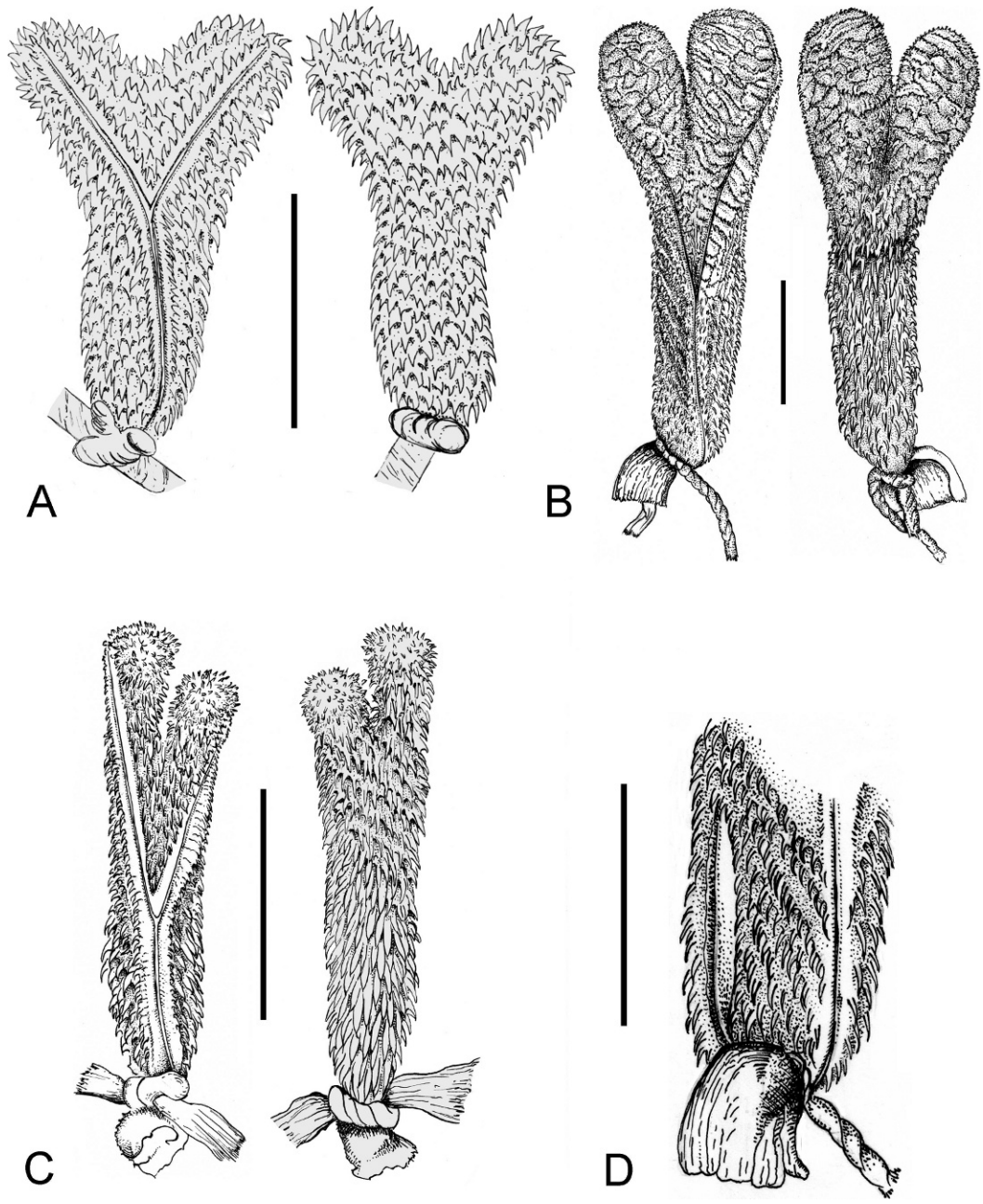

FIG. 4.—Sulcate (left) and asulcate (right) sides of the hemipenis of *Atractus occipitoalbus* (A), *Atractus duboisi* (B), *Atractus orcesi* (C), and detailed view of the basal naked pocket of the hemipenis of *A. duboisi* (D). (Scale = 5 mm.)

410 mm and males 388 mm SVL; (15) moderate tail in females (6.7–10.0% SVL) and moderate to long (13.3–20.4% SVL) in males; (16) hemipenis moderately bilobed, semicapitate, and semicalyculate.

Comparisons.—*Atractus duboisi* differs from all 15 dorsal scale row *Atractus* by having a black or dark brown dorsum, with paired light (creamish yellow) blotches (generally 1 scale wide) and a wide longitudinal midventral dark

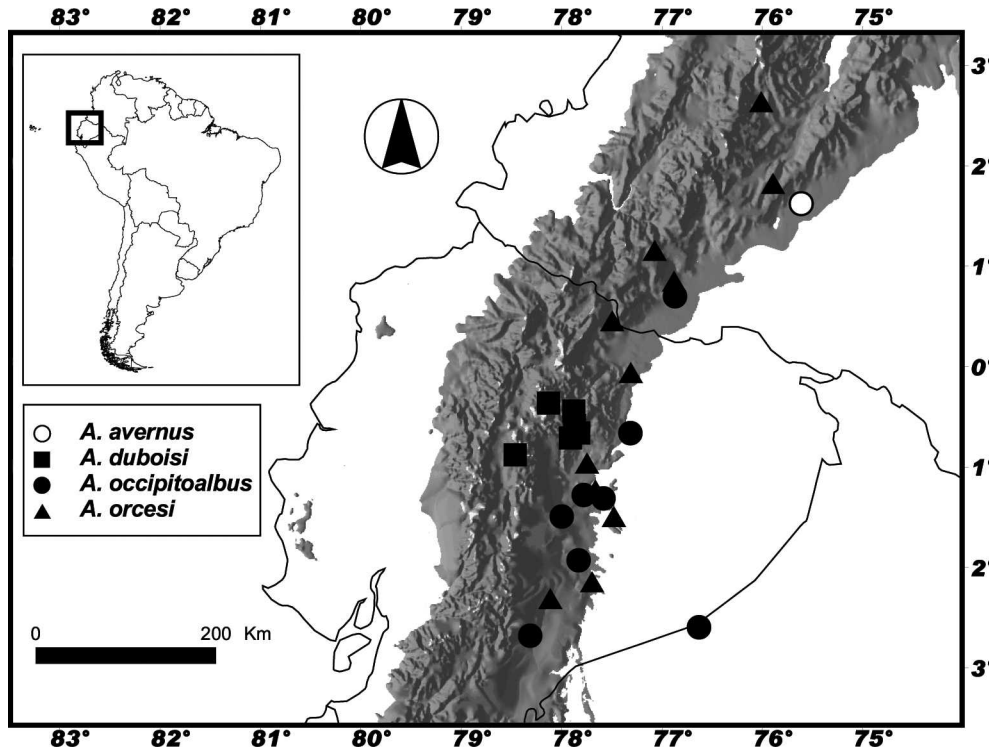

FIG. 5.—Geographical distribution of *Atractus avernus*, *A. duboisi*, *Atractus occipitoalbus*, and *Atractus orcesi*.

stripe. Melanic specimens of *A. duboisi* that have no paired light blotches are very similar to melanic specimens of *A. orcesi*, but differ from it by lacking light band on occipital region and dorsolateral stripes, curved head in lateral view, and hemipenis with well marked capitular groove (vs. light band on occipital region, dorsolateral stripes, flattened head in lateral view, and hemipenis without capitular groove). Melanic individuals of *A. duboisi* differ from *A. occipitoalbus* by lacking wide occipital white band, having venter creamish-white with wide black stripe, and semicapitate hemipenis (vs. broad occipital white band, venter uniformly black, and non capitate hemipenis).

Description.—Head with barely distinct cervical constriction, arched in lateral view, round in dorsal view, twice as long as wide; snout truncate or slightly acuminate in lateral view, round in dorsal view; rostral sub-triangular in frontal view, generally not visible from above, broader than high; internasal longer than wide; internasal suture sinistral with respect to prefrontal suture; prefrontal longer than wide; supraocular twice as long as wide; frontal sub-pentagonal in dorsal view, broader than long; parietal about twice as long as wide; nasal divided; nostril located between prenasal and postnasals; prenasal twice as high as long; postnasal twice as high as long; loreal long, generally contacting 2–4th supralabials; pupil round; 2 postoculars similar in size; temporals 1+2; anterior temporal twice as long as high; upper posterior temporal elongate, 3 times longer than wide; usually 8 supralabials, 4–5th contacting orbit; 2nd and 3rd supralabials similar in size, slightly higher than first supralabial; frequently 4th supralabial higher and 8th one longer than remaining supralabials; symphisial semicircular, approximately 6 times as broad as long; generally 7 infralabials, first 4 in contact with chinshields; first pair of infralabials in contact behind symphisial, preventing symphisial-chinshields contact; chinshields 3 times as long as wide; usually 4 gular scale rows; generally 4 preventrals; 15/15/15 dorsal scale rows; dorsals smooth, without apical pits,

supranal tubercles, and keels; caudal spine moderate, conical, robust, and rhomboid; maxilla arched in dorsal view, with 5–6 prediastemal and 1–2 postdiastemal teeth; prediastemal teeth large, robust at the base and narrowed on the apices, angular in cross section; prediastemal teeth moderately spaced, curved, and slightly decreasing in size posteriorly; maxillary diastema moderate; postdiastemal teeth smaller than last prediastemal teeth; lateral process of the maxilla poorly developed, lacking posterior projection.

Color pattern in preservative.—Dorsum of head uniform dark brown or black, except for a few light brown diffuse spots; dorsal and lateral background of head dark brown or black, with ventral portion of supralabials light anteriorly; infralabials and gular region spotted with dark brown dots, mostly on the anterior portion of each scale; ventral scales with dark edges; wide longitudinal dark midventral stripe; lateral ends of ventral scales cream, forming a narrow longitudinal stripe on each side of the dark midventral stripe; dorsal background color of body uniformly dark brown or black, except for light (creamish yellow) paired blotches (generally one scale wide) between 5–6th dorsal scale rows; sometimes the light center of the first dorsal scale row (on both sides) forms an ill-defined longitudinal light stripe (Fig. 6).

Hemipenis.—Inverted organ bifurcates at 8th and extends to level of 10th subcaudal. Fully everted and almost maximally expanded hemipenis rendered a bilobed, semicapitate, and semicalyculate organ; capitular groove well marked on the asulcate side, and barely defined on the sulcate and lateral sides; capitular groove located just above sulcus bifurcation; lobes restricted to distal half of capitulum, uniformly covered by small and shallow papillate calyces; papillae progressively replaced by spinules toward base of capitulum; calyces tend to lose their vertical walls and form defined flounces on the median to distal portion of capitulum in sulcate side; each lobe slightly distinct from base, with a clavate form, nearly rounded on the apical portion; lobes approximately the same size; sulcus spermaticus divides about half of organ; branches have centrifugal orientation terminating on the tip of the lobes; margin of sulcus spermaticus stout, bordered by series of spinules from the base of organ to the crotch of lobes; hemipenial body uniformly covered by medium-size hooked spines; basal naked pocket longer than wide located laterally on the basal portion of hemipenial body; most basal portion of hemipenial body nude, except for some dispersed spinules (Fig. 4B, D).

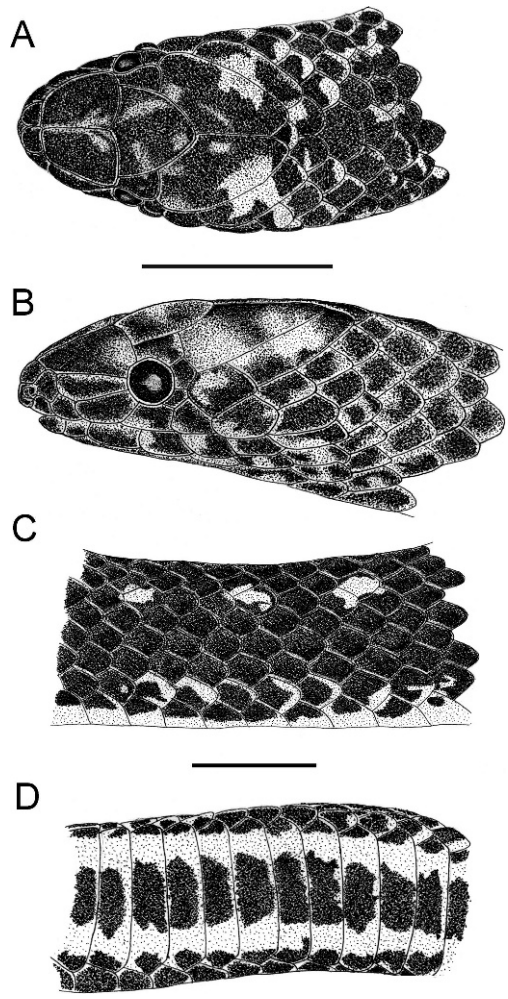

FIG. 6.—Dorsal (A) and lateral (B) views of the head, and dorsal (C) and ventral (D) views of the body of *Atractus duboisi* (QCAZ 2106). (Scale = 5 mm).

Variation.—Largest male 388 mm SVL, 69 mm CL; largest female 410 mm SVL, 31 mm CL; tail 13.3–20.4% ($\bar{x}$ = 16.7, SD = 2.0, n = 15) of the SVL in males and 6.7–10% ($\bar{x}$ = 7.8, SD = 0.7, n = 20) of the SVL in

females; ventrals 150–167 ($\bar{x}$ = 158, SD = 3.5, n = 43) in males, 159–172 ($\bar{x}$ = 166, SD = 3.2, n = 54) in females; subcaudals 23–36 ($\bar{x}$ = 31.6, SD = 2.3, n = 43) in males, 13–21 ($\bar{x}$ = 16.8, SD = 1.5, n = 53) in females; 7–9 ($\bar{x}$ = 7.5, SD = 0.4, n = 122 sides) supralabials; 6–7 ($\bar{x}$ = 6.9, SD = 0.2, n = 122 sides) infralabials; 1–3 (n = 15 sides), 1–4 (n = 102 sides) or 1–5 (n = 2 sides) infralabials contacting chinshields; 3–4 ($\bar{x}$ = 3.8, SD = 0.3, n = 122 sides) gular rows; 3–5 ($\bar{x}$ = 4.0, SD = 0.3, n = 122 sides) preventrals; 6–10 ($\bar{x}$ = 8.1, SD = 0.6, n = 60) dorsal scales of the tail; hemipenis bifurcates at 7th–12th and extends to the level of 9th–14th subcaudal ($\bar{x}$ = 11.2, SD = 3.2, n = 2).

Distribution.—*Atractus duboisi* is known only from Cordillera Real on the Atlantic versant of the Andes, occurring from Baeza (00° 27′ S, 77° 53′ W) to Cordillera de Guacamayos (00° 43′ S, 77° 55′ W) in the Napo Province of Ecuador. This species inhabits the Mountain Cloud Forest formation, and occurs at elevations between 1500–2200 m (Fig. 5).

Remarks.—The holotype (photographs analyzed) of *Rabdosoma duboisi* is well preserved and has the same color pattern as the specimens examined here (i.e., dark brown dorsal background with paired light blotches arranged longitudinally and wide dark midventral stripe). Further, the ventral and subcaudal counts and tail length observed on the type pictures is in agreement with our sample. Therefore, the name *A. duboisi* should be employed to the specimens from Napo/Baeza provenance.

Atractus orcesi *Savage, 1955* *(Status revalidated)*

Atractus orcesi Savage, 1955; Proceedings of the Biological Society of Washington 68:17.

Atractus occipitoalbus – Savage 1960; Miscellaneous Publication of the Museum of Zoology, University of Michigan 112:60 (part).

Holotype.—Adult male, CAS-SU 15622, from Loreto (00° 40′ S, 77° 19′ W, ca. 450 m), Province of Orellana, Ecuador, collected on October 1952 by J. Olalla (specimen examined).

Diagnosis.—*Atractus orcesi* can be distinguished from all congeners by the following combination of characters: (1) 15/15/15 dorsal scale rows, without apical pits, supranal tubercles, and keels; (2) 2 postoculars; (3) loreal moderate; (4) temporals 1+2; (5) generally 8 supralabials, 4–5th contacting orbit; (6) generally 7 infralabials, first 4 in contact with genials; (7) 7–9 maxillary teeth; (8) 3–4 gular scale rows; (9) 3–4 preventrals; (10) 142–158 ventrals in females and 134–152 in males; (11) 13–22 subcaudals in females and 18–34 in males; (12) dorsal color pattern dark brown, with a creamish brown occipital band, and vertebral and dorsolateral stripes; (13) venter with a median black large stripe; (14) small body size, females reaching 274 mm and males 239 mm; (15) small to moderate tail sizes in females (7.1–9.4% SVL) and males (11.2–17.1% SVL); (16) hemipenis moderately bilobed, non capitate, and semicalyculate.

Comparisons.—Among all *Atractus* species with 15 dorsal scale rows, *Atractus orcesi* shares a midventral stripe and band on the occipital region only with some specimens of *A. boettgeri* and *A. taeniatus*, but differs from these by having 7–8 supralabials and lateral stripes on the flanks (vs. 6 supralabials and no lateral stripes on the flanks). Additionally, it differs from the other species of *Atractus* with 15 dorsal scale rows (*A. albuquerquei*, *A. boettgeri*, *A. duboisi*, *A. edioi*, *A. emmeli*, *A. erythromelas*, *A. occipitoalbus*, *A. paraguayensis*, *A. meridensis*, *A. reticulatus*, *A. paraguayensis*, *A. taeniatus*, *A. tamessari*, *A. ventrimaculatus*, *A. vittatus*), except *A. trilineatus*, that lack lateral stripes on the flanks. *Atractus orcesi* differs from *A. trilineatus* by having 7 maxillary teeth, 2 postdiastemal teeth, and a midventral dark brown stripe (vs. 6 maxillary teeth, one postdiastemal teeth, and uniform creamish white venter in preservative). Melanic specimens of *A. orcesi* can be easily distinguished from *A. duboisi* by lacking capitular groove and well defined vertical walls of the calyces (vs. semicapitate organ having well defined vertical walls of calyces); from *A. occipitoalbus* by having creamish white venter with wide midventral black stripe, two postoculars, and hemipenial calyces slightly developed (vs. uniformly black venter, single postocular, and lacking calyces).

Description.—Head lacking cervical constriction, sub-triangular in dorsal view, flat-

tened in lateral view, twice as long as wide; snout round in dorsal, slightly acuminate in lateral view; rostral sub-triangular in frontal view, little visible from above, broader than high; internasal longer than wide; internasal suture sinistral with respect to prefrontal suture; prefrontal longer than wide; supraocular sub-rectangular, twice as long as wide; frontal sub-triangular or pentagonal, longer than wide; parietal approximately twice as long as wide; nasal divided; nostril located between prenasal and postnasals; prenasal about twice as high as long; postnasal as long as wide; loreal moderate, contacting 2nd and 3rd supralabials; pupil round; postoculars similar in size; temporals 1+2; anterior temporal twice as long as wide; upper posterior temporal elongate, 3 times longer than wide; generally 8 supralabials, 4–5th contacting orbit; 2nd and 3rd supralabials similar in size and higher than first supralabial; 4th higher than first 3 supralabials; 6th higher and 8th supralabial longer than remaining; symphisial subtriangular, twice as broad as long; generally 7 infralabials, first 4 in contact with genials; first pair in contact behind symphisial, preventing symphisial/genials contact; generally 3 gular scale rows; 3–5 preventrals; 15/15/15 dorsal scale rows; dorsals smooth, without apical pits, supranal tubercles, and keels; caudal spine moderate, conical, and slightly acuminate; maxilla arched in dorsal view, with 5–7 prediastemal and 2 postdiastemal teeth; prediastemal teeth large, robust at base and acuminate on the apices, angulars in the cross section; prediastemal teeth moderately spaced, curved posteriorly; postdiastemal teeth having half size of the prediastemal ones; lateral process of maxillary poorly developed, lacking posterior projection.

Color pattern in preservative.—Dorsum of head dark brown to black, except for an incomplete creamish white occipital band generally located at mid to posterior portion of parietals; lateral background of head dark brown, with ventral portion of supralabials light posteriorly; dorsal portion from 6–8th supralabials generally dark brown forming a narrow postocular stripe; mental region generally uniform creamish white; preventrals black; ventral ground color creamish white, with a large median black stripe; edges of ventral scales creamish white, constituting a paraventral light stripes; median stripes occupying two-thirds of venter area; dorsum of body brown to dark brown, usually with dark brown vertebral (1 scale wide) and dorsolateral lines (1 scales wide) on the 2nd and 3rd dorsal scale rows; eventually center of first dorsal scale row light, located just between the dorsolateral and paraventral stripes (Fig. 7).

Hemipenis.—Inverted organ bifurcates at 8th and extends to level of 9th subcaudal. Fully everted and almost maximally expanded hemipenis rendered a bilobed, non capitate, and semicalyculate organ; capitular groove slightly marked on the asulcate side, and barely defined on the sulcate and lateral sides; capitular groove located just bellow sulcus bifurcation; lobes restricted to distal half of weakly distinct *capitulum*, uniformly covered of small and shallow spinulate calyces; calyces tend to lose their vertical walls and form poorly defined flounces; each lobe slightly distinct from base, with a clavate form, nearly flattened on apical portion; left lobe considerably longer than right; sulcus spermaticus divides about half of organ; branches have centrifugal orientation terminating on the tip of the lobes; margin of sulcus spermaticus stout, bordered by moderate spinules from the base of organ to the tips of lobes; hemipenial body uniformly covered by medium-size hooked spines; large spines concentrated on the median portion of asulcate and lateral portions of sulcate side; basal naked pocket longer than wide located laterally on the basal portion of hemipenial body; most basal portion of hemipenial body nude, except for some dispersed spinules (Fig. 4C).

Variation.—Largest male 239 mm SVL, 36 mm CL; largest female 274 mm SVL, 24 mm CL; tail 11.2–17.1% ($\bar{x}$ = 14.3, SD = 1.5, n = 20) of the SVL in males and 7–9.4% ($\bar{x}$ = 8.5, SD = 0.8, n = 18) in females; 134–152 ($\bar{x}$ = 145.5, SD = 6.3, n = 20) ventrals in males and 142–158 ($\bar{x}$ = 151.2, SD = 4.9, n = 18) in females; 18–34 ($\bar{x}$ = 28, SD = 3.4, n = 20) subcaudals in males and 13–22 ($\bar{x}$ = 19.4, SD = 2, n = 18) in females; 7 (n = 7 sides) or 8 (n = 69 sides) supralabials; 7 (n = 77 sides) or 8 (n = 5 sides) infralabials; 1–4 (n = 80 sides) or 1–5 (n = 2 sides) infralabials contacting chinshields; 3 (n = 8 sides) or 4

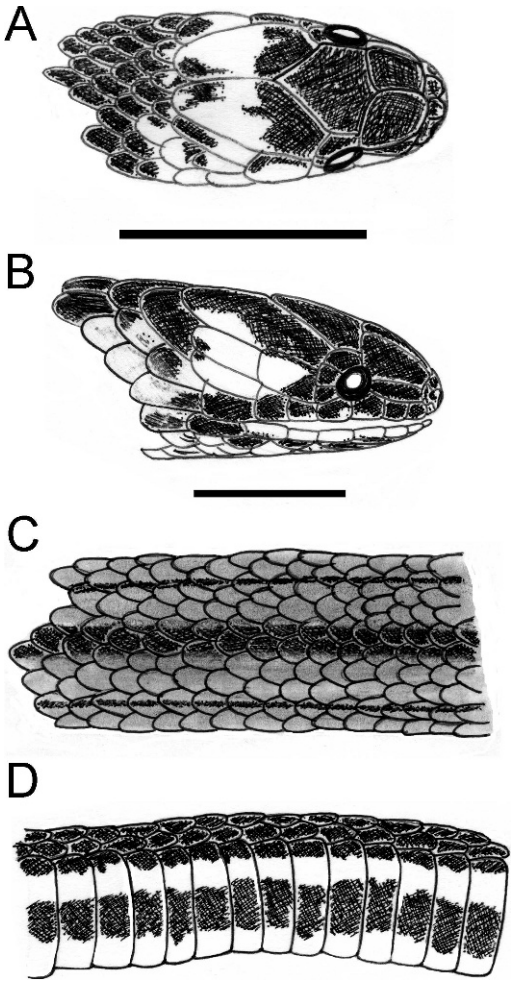

FIG. 7.—Dorsal (A) and lateral (B) views of the head, and dorsal (C) and ventral (D) views of the body of *Atractus orcesi* (USNM 237722). (Scale = 5 mm).

(n = 7 sides) gular scale rows; 3 (n = 3), 4 (n = 5) or 5 (n = 1) preventrals; 6–10 ($\bar{x}$ = 7.9, SD = 0.8, n = 20) dorsal scale rows in the level of 2nd subcaudal; 7 (n = 32 sides), 8 (n = 6 sides) or 9 (n = 2 sides) maxillary teeth; retracted hemipenis extend to the level of 9th subcaudal (n = 1).

Distribution.—*Atractus orcesi* occurs in the Amazon versant of the Andes from Parque Nacional Cueva de Los Guacharos (01° 49′ N, 75° 53′ W) in the Department of Cauca, Colombia, to Macas (02° 19′ S, 78° 07′ W) in the Province of Morona-Santiago, Ecuador. This species inhabits Amazon Most Broadest Forest and Andean Broadest Forest between 500–3000 m (Fig. 5).

Remarks.—The faded color pattern of the holotype of *Atractus orcesi* preserves the vertebral line and lateral stripes that permit the association of this taxon with the sample considered herein. However, *A. orcesi* as defined here could represent a polytypic species, with the population from geographical extremes representing two distinct species, but more specimen and locality samples are necessary to evaluate the taxonomic status of some populations herein included within *A. orcesi*.

Atractus avernus *sp. nov.*

Holotype.—Adult female, MLS 2725, collected by Brother Niceforo Maria at locality of Paraíso (01° 14′ N, 75° 37′ W, ca. 480 m), municipality of Florencia, Department of Caquetá, Colombia.

Diagnosis.—*Atractus avernus* can be distinguished from all congeners by the following combination of characters: (1) 15/15/15 dorsal scale rows, smooth, without apical pits and keels; (2) 2 postoculars; (3) long loreal; (4) temporals 1+2; (5) 7 supralabials, 3rd and 4th contacting orbit; (6) 7 infralabials, first 4 contacting chinshields; (7) 5 prediastemal and 2 postdiastemal maxillary teeth; (8) 3 gular scale rows; (9) 4 preventrals; (10) 135 ventrals on the single female; (11) 10 subcaudals; (12) dorsal color pattern dark brown with a creamish white occipital band, and paravertebral paired light dots along body; (13) venter creamish white and tail uniform black; (14) small size, only female reaching 168 mm; (15) short tail in the female (5.3% SVL).

Comparisons.—Among all congeners, *Atractus avernus* shares only with *A. occipitoalbus* the following combination of characters: 15/15/15 dorsal scales rows, light occipital band, dorsal color pattern dark brown, number of subcaudal scales below 20, small body (<300 mm) and tail (<10% SVL) sizes. The new species differs form *A. occipitoalbus* by having 7 supralabials, 2 postoculars, 135 ventrals, dorsal color pattern dark brown uniformly pointed by cream small dots, and venter uniformly creamish white (vs. generally eight supralabials, one postocular scale in females, 142–172 ventrals in females, dorsal

color pattern dark brown or uniform black, and venter uniformly black).

Description of holotype.—Adult female, SVL 168 mm, CL 9 mm (5.3% of SVL); body diameter 2.9 mm (1.7% of SVL); head length 6.6 mm (3.9% of SVL); head width 3.1 mm (51% of head length); interocular distance 2.7 mm; rostrorbital distance 2.1 mm (75% interocular distance); nasorbital distance 1.4 mm; cervical constriction indistinct, head shape arched in lateral view, sub-triangular in dorsal view; snout truncate in lateral view, round in dorsal view; rostral sub-triangular in frontal view, barely visible from above, 1.1 mm width, 0.6 mm high; internasal 0.6 mm length, 0.5 mm width; internasal suture sinistral with respect to prefrontal suture; prefrontal 1.4 mm length, 1.3 mm width; supraocular 0.7 mm length, as long as wide; frontal sub-triangular in dorsal view, 2.0 mm length, 1.9 mm width; parietal 3.3 mm length, twice as long as wide; nasal divided; nostril located between pre-nasal and postnasals; postnasal 0.4 mm, as high as long; loreal 1.0 mm length, 0.3 mm high, contacting 2nd and 3rd supralabials; eye diameter 1.0 mm; pupil round; 2 postoculars; upper postocular (0.3 mm high, 0.6 mm length) longer than postocular lower postocular; temporals 1+2; upper posterior temporal elongate (2.5 mm), approximately 5 times as long as high; 7 supralabials, 3rd and 4th contacting orbit; first supralabial smaller than 2nd, and equivalent to 3rd supralabial; 6th supralabial higher and longer than the other supralabials; symphisial 0.7 mm wide, twice as broad as long; seven infralabials, first 4 in contact with chinshields; first pair of infralabials in contact behind symphisial, preventing symphisial/genials contact; chinshields 2.0 mm length, 4 times as longer as wide; 3 gular scale rows; 4 preventrals; 135 ventrals; 10 subcaudals; 15/15/15 dorsal scale rows; dorsals smooth, without apical pits, supranal tubercles, and keels; 6 dorsal scale rows in the level of 2nd subcaudal; maxilla flattened in dorsal view, with 5 prediastemal and 2 postdiastemal teeth; prediastemal teeth large, angular in the cross section, robust at the base and narrowed on the apices; prediastemal teeth curved posteriorly, and moderately spaced; maxillary diastema moderate.

Color pattern of the holotype.—Dorsum of head dark brown, with diffuse light brown dots on the center of cephalic plates, and creamish white occipital band; occipital band extends from mid-portion to end of parietals; head laterally uniform dark brown, except for temporal and occipital regions uniform creamish white; first 5 supralabials uniformly dark brown; 6th and 7th creamish white; infralabials and mental region predominantly creamish white; 3rd to 5th infralabials dark pigmented along with the chinshields suture; chinshields with dark brown blotches anteriorly; venter creamish white, except for lateral margin of ventral scales dark brown pigmented; tail uniform dark brown; dorsal ground color of body dark brown, with a series of 56/57 paired, small (1 scale width and long), light dots on the paravertebral region; first dorsal scale row with beige center, forming a barely conspicuous light stripe ventrally delimited by the dark edges of ventral scales (Fig. 8).

Etymology.—The specific epithet *"avernus"* is a Latin word meaning the nether world or infernal regions of the earth. This name is used herein in allusion to the apparent secretive habits of the new species.

Distribution.—Known only from the locality of Paraiso, municipality of Florencia, Caquetá Department, Colombia. *Atractus avernus* probably occurs along Amazon Rainforest, which covered most of Caquetá Department (Fig. 5).

Discussion

Savage (1960) synonymized *Atractus duboisi* and *A. orcesi* with *A. occipitoalbus* based on the absence of unambiguous diagnostic characters to recognize them, interpreting differences in color pattern as distinct stages in their range of variation (Savage, 1960, op. cit.). Although we have found a complex pattern of distribution principally for ventral coloration, the present study revealed that noticeable divergent color patterns (mainly from dorsum of head and body) hold a geographic basis that do not overlap along their range (Figs. 3, 6, 7–8). Moreover, these distinctive color patterns were congruent with other qualitative (Fig. 4) and quantitative (Fig. 1, Tables 1, 3) features for each recognized taxon.

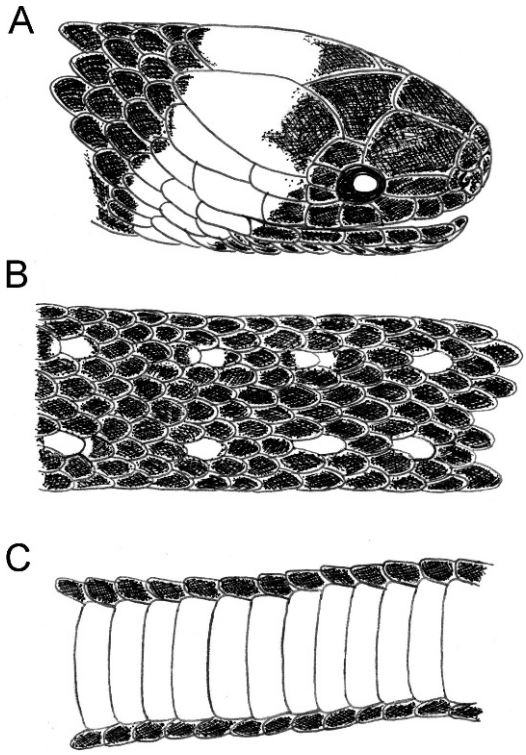

FIG. 8.—Lateral view of the head (A), and dorsal (B) and ventral views of the body of the holotype of *Atractus avernus* (MLS 2725). Line arts were based on specimen photographs.

The quantitative analyses of meristic and morphometric variables corroborate the qualitative differences of the species. The females DFA reveal that *A. occipitoalbus* was distinguished from *A. duboisi* and *A. orcesi* mainly by number of subcaudal and postocular scales, whereas both differ from each other mainly in the number ventral, chinshields, and gular scales (Fig. 2B, Table 2). The robustness of DFA was guaranteed by no overlapping of the confidence ellipses in the morphometric space after 1,000 bootstrap replicates performed (Fig. 1A). Although DFA for males cannot separate entirely *Atractus duboisi* from *A. orcesi* based on the number of ventral scales and SVL/CL ratio, the post-hoc comparisons found significant differences between both species and classificatory matrix of DFA for male populations obtained about 95% of corrected classification of individuals within previously defined populations (Table 3). Yet, directional cosines show those DFA variables having lower variance magnitude were responsible by some best discriminant function among male populations (Fig. 2B). As such, it could be expected that a small overlap of low variance characters strongly correlated with principal axis from DFA produces disparate classified individuals in the multivariate space.

The concordance between at least two apparently fixed diagnostic morphological characters has been used, on morphological studies, as a robust operational criterion to species delimitation (Jorge da Silva and Sites, 1999; Passos and Fernandes, 2009). Nevertheless, Wiens and Servedio (2000) proposed a more realistic method in which the statistical confidence is assessed for a single putative truly fixed diagnostic feature. However, This procedure is very sensitive to character and specimen sample size (Passos and Fernandes, 2009; Wiens and Servedio, 2000). In the absence of accurate sample size to achieve statistical significance of the diagnostic characters, we realize that the concordance approach between discrete and continuous apparently uncorrelated variables can also provide a robust support to species delimitation.

Atractus avernus and *A. duboisi* are allopatric taxa, with Putumayo and Caquetá Rivers (*A. avernus*) and the Cordillera de Guacamayos (*A. duboisi*) apparently acting as a barrier between each other and between *A. occipitoalbus* and *A. orcesi* populations (Fig. 5). *Atractus avernus* is known only from the type locality and *A. duboisi* is restricted to the mountain cloud forest at Cordillera Real of Ecuador, while *A. occipitoalbus* and *A. orcesi* occur in the upper Amazon basin at rain and riparian forests. According to our sample, the latter two species have a parapatric distribution on the Amazon versant of the Andes (Fig. 5). *Atractus orcesi* occurs primarily at higher elevations (above 1000 m) on the Andes, whereas *A. occipitoalbus* is restricted to Amazon lowlands or riparian forest of the rivers originating on the Andes (Fig. 5). Since many strictly Amazon *Atractus* (e.g., *A. elaps* and *A. snethlageae*) share the same pattern of distribution, we hypothesize that gallery forests of the Rivers propitiate dispersal of lowland species to Andean headwater. This scenario may explain some of the actual sympatric zones for some closely related species on Amazon rainforest.

Resumo

O posicionamento taxonômico de *Atractus occipitoalbus* é revisado por meio da concordância entre as análises quantitativa e qualitativa de caracteres morfológicos (merísticos, morfométricos, padrões de colorido e hemipênis). *Atractus duboisi* e *A. orcesi* são aqui revalidadas baseado no número de escamas ventrais e subcaudais, número de escamas pós-oculares, forma da cabeça em vista lateral, comprimento relativo da cauda, padrões de coloração distintos e morfologia hemipeniana. Adicionalmente, uma nova espécie, proximamente relacionada à *A. occipitoalbus*, é descrita do piemonte andino da Colômbia. A espécie nova, representada somente por uma fêmea, é diagnosticada das populações de fêmeas de *A. occipitoalbus* por meio do número de subcaudais, número de escamas pós-oculares e do padrão de coloração ventral e dorsal.

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Appendix I

Specimens Examined

Atractus albuquerquei (*n* = 13).—**BRAZIL:** GOIÁS: Aporé: UHE Aporé: (MNRJ 14370–76); PARÁ: Orilândia: (MPEG 20792), Vila Nova: Tomé-Açu-Paragominas road, near Rio Timboteua: (MPEG 12946, holotype); RONDÔNIA: Porto Velho: UHE Samuel: (CHUFC 1482–84), Vila Cachoeira do Samuel: (MNRJ 3028).

Atractus biseriatus (*n* = 1).—**COLOMBIA:** CALDAS: Villamaria: (MLS 145, holotype).

Atractus boettgeri (*n* = 1).—**BOLIVIA:** COCHABAMBA: Yungas: (NHM 1946.1.6.29 holotype).

Atractus carrioni (*n* = 13).—**ECUADOR:** LOJA: Loja: (QCAZ 793, 1081–82, 1217–18, 6445–46, EPN 8673–74), Yangana: (QCAZ 684), Loja dos Puentes: Río Molacatus: (QCAZ 6533–34).

Atractus charitoae (*n* = 1).—**COLOMBIA:** AMAZONAS: Vaupés: Taraira: (ICN 10095, holotype).

Atractus duboisi (*n* = 99).—**ECUADOR:** NAPO: Unknown locality: (EPN four specimens not catalogued), Baeza: (KU 142929–36, 146713–32, 189933, QCAZ 1234–1241, 2103, 2759, 4110, 4156), Cantón Quijos: (EPN 1281–89, 3121), Baeza-Quito road: (QCAZ 4195, 4201), Cordillera Guacamayos (EPN 6875, QCAZ 3707–08, 3290), Cosanga: (QCAZ 906, 2098, 2106–07, 2759, 2798–2806, 5469), Hollin:Vía Loreto: (QCAZ 2104), Las

Palmas: (QCAZ 3347–3350, 6593–95), Napo: (QCAZ 2797), Papallacta: (KU 218415), Quijos Valley: (USNM 232540, 232543–45, 232547).

Atractus elaps (*n* = 77).—**BRAZIL:** Unknown locality: (IBSP 20314); AMAZONAS: Borba: (MNRJ 1523). **COLOMBIA:** Unknown locality: (MLS 182); AMAZONAS: Parque Natural Nacional Amacayacu: (IAvH 3211); BOYACÁ: Macanal: (MLS 2637); CAQUETÁ: Unknown locality: (MLS 183); Florencia: (MLS 185, 187, 195, 197, 1316–18, 1322–23, 1326–27, 1739, 2730, 2733–39); CAUCA: Santa Rosa: El Carmen: (IAvH 4410); CUNDINAMARCA: Medina: (MLS 192), Sasaima: (MLS 2527), Guaicarano: Paratebueno: (MLS 188); META: Acacias: (MLS 191), San Juan de Arama: (IAvH 929), Villavicencio: (MLS 179, 189, 193, 196, 266, 1396, 2054–55), Rio Ocoa: Villavicencio: (MLS 190); PUTUMAYO: Unknown locality: (MLS 180). **ECUADOR:** Eastern Ecuador: Unknown locality: (EPN 6892, EPN not cataloged); NAPO: Upper Río Napo: (EPN 6856, 8686), Archidona: (QCAZ 2101), Río Huataracu: (EPN 8687); ORELLANA: Balsayacu: Parque Sumaco: (QCAZ 6502), Fuerte: (EPN 7324), Loreto: El Tená: (EPN 8688), Parque Nacional Yasuní: (EPN 2536, QCAZ 3249, 3959), Río Coca: (QCAZ 440); PASTAZA: Mera: (EPN 1175), Montalvo: Andoas: (EPN 758), Nueva Vida: Misión Agua Santa: (QCAZ 345), Puyo: (QCAZ 1277), Río Bobonaza: (EPN 8678–83), Río Tallín: Upper Bobonaza: (EPN 8675–77), Sarayacu–Pucayacu: (EPN 8685); SUCUMBÍOS: Lagartococha: (EPN 8689), Lago Ágrio: (EPN 5781), Shushufindi: (QCAZ 3303); Erroneous localities: Pichincha: Al Occidente: (EPN 8692); El Oro: Santa Rosa: (EPN 8690–91).

Atractus emmeli (*n* = 14).—**BOLIVIA:** BENI: Yacuma: Estación Biológica Beni: (CBF 434), Ballivián: San Marcos: Río Negro: (MNKR 3718–19); LA PAZ: Iturralde: (CBF 765), Maldidi: (CBF 758), Laguna Piraña: (CBF 2321), Franz Tamayo: Yariapo: (CBF 2288), Moxos: San Lorenzo: (CBF 992). **PERU:** Unknown locality: (MHNSM 2313); CUSCO: Convención: Camisea: (MHNSM 3467); LORETO: Coronel Portillo: Pucallpa: (MHNSM 2653, 3101); JUNÍN: Tarma: Yurinaqui Alto: (MHNSM 2644, 11144).

Atractus erythromelas (*n* = 9).—**VENEZUELA:** MÉRIDA: Libertador: (MHNLS 902), Mérida: (NHM 1.716–17 paratypes, CSJ 519), Mucurubá: (MHNLS 276–78, 630, 902).

Atractus franciscopaivai (*n* = 3).—**COLOMBIA:** Amazonas: La Pedrera: (ICN 10100 holotype, 10101–02 paratypes).

Atractus heliobelluomini (*n* = 1).—**COLOMBIA:** AMAZONAS: La Pedrera: (ICN 10103, holotype).

Atractus insipidus (*n* = 1).—**VENEZUELA:** AMAZONAS: Poste M-1: Rio Araricapará: Venezuelan-Brazil border: (MBUCV 3957, holotype).

Atractus manizalensis (*n* = 21).—**COLOMBIA:** CALDAS: Manizales: (IAvH 3309–10, MLS 294), Pacorá: (MLS 2216), Villamaria: (MLS 227 holotype, MLS 228 paratype, MLS 146, 2461, 1999), Salamina: (MLS 173, 226, 1777, 1779–80, 2716); QUINDIO: Armenia: (UQC 01, 05, 08, 03 specimens not catalogued at UQC).

Atractus meridensis (*n* = 10).—**VENEZUELA:** MÉRIDA: Las Piedras: Río Santo Domingo: Pueblo Llano: (ULABG 4341 holotype, 4694–96 paratypes); Libertador: (ULABG 4090–91, 4408, 4941, paratypes); Mérida: (ULABG 4154, paratype); Parque Chorros: (ULABG 2533, paratype).

Atractus nicefori (*n* = 16).—**COLOMBIA:** ANTIOQUIA: Jardin: (MLS 2940), Jericó: (MLS 229, MLS 231–33, 239–40, 275, 279, 297, 302, 2635–37), Támesis: (MUJ 02–03).

Atractus occipitoalbus (*n* = 30).—**COLOMBIA:** PUTUMAYO: El Orito (ICN10116). **ECUADOR:** MORONA-SANTIAGO: Chiguaza: (USNM 232697), Río Nepano: Mendez (EPN 8729); NAPO: Santa Cecilia: (KU 109832), Puerto Libre: Río Aguarico: (KU 121842–43, 121845–49); ORELLANA: Loreto: (USNM 232694–95); PASTAZA: Arajuno: Upper Río Napo: (EPN 8719–20), Upper Río Arajuno: (USNM 234808, 234701), Río Bobonaza (EPN 8724–27, USNM 234812, 234814), Upper Río Oglan: (USNM 234809), Upper Río Curaray (EPN 8721–22, USNM 234807, 234811), Puyo: Hosteria Turingia: (USNM 205030), Puyo: Santana: (EPN 6474).

Atractus ochrosetrus (*n* = 2).—**VENEZUELA:** MERIDA: Tovar: (ULABG 4698, holotype; 4696, paratype).

Atractus oculotemporalis (*n* = 1).—**COLOMBIA:** ANTIOQUIA: Jericó: (IBSP 6390 holotype).

Atractus orcesi (*n* = 41).—**COLOMBIA:** CAUCA: Santa Rosa: Vereda El Cajor: (IAvH 4704); HUILA: Acevedo: Parque Natural Nacional Cueva de los Guacharos: (IAvH 3105); PUTUMAYO: Valle Sibundoy: Santiago: Vereda Balsayaco: (ICN 10803–04). **ECUADOR:** MORONA-SANTIAGO: between Chiguaza and Macuma: (USNM 232696), Estrada Limón-Macas: (QCAZ 7263–64); NAPO: Upper Río Arajuno: (EPN 8723, USNM 232700), Río Hollio: (QCAZ 6268); ORELLANA: Loreto: (CAS-SU 15622, holotype); PASTAZA: Río Villano: (USNM 232702–04, 232706), Upper Río Bobonaza: (USNM 232699); SUCÚMBIOS: La Bonita: (QCAZ 2779, USNM 232707–22), Lago Agrio: (KU 125999–05).

Atractus cf. *paraguayensis* (*n* = 42).—**BRAZIL:** PARANÁ: Pinhão: Rio Jordão (MCP 7185, 7211, 7364–65); RIO GRANDE DO SUL: Carazinho: (CRUPF 1180), Colorado: (CRUPF 1196); Derrubadas: Parque Florestal Estadual do Turvo: (MCP 12387), Getúlio Vargas: (CRUPF 64); Giruá: (IB 10380), Ibirapuitã: (CRUPF 587), Ijuí: (MCP 13726–32), Mato Castelhano: (CRUPF 289, 516, 992, 1094), Pinheiro Machado: (CRUPF 257), Planalto: (MCP 5898–99, 5915, 5997), Porto Mauá: (MCP 11609, 11611, 11623), Porto Vera Cruz (MCP 11670), Santo Ângelo: (IB 9552, MCP 12516–17), Tapejara: (CRUPF 417, 814); SANTA CATARINA: Chapecó: (MCP 14013), Concórdia: Entre Rios: (MCP 2912), Ipira: (MCP 2913), Peritiba: (MCP 2939), Piratuba (MCP 2893–94, 2902).

Atractus poeppigi (*n* = 8).—**COLOMBIA:** AMAZONAS: Letícia: (MLS 133, 1313–15, MUJ 89). **PERU:** AMAZONAS: Bagua: (MHNSM 2380, 2447); PASCO: Oxapampa: Cerro de Pasço: (MHNSM 3485).

Atractus potschi (*n* = 18).—**BRASIL:** ALAGOAS: Maceió: (IBSP 48438, holotype); BAHIA: Feira de Santana: Jaíba: (MZUEFS 454), Fazenda Brasileiro: (MZUEFS 682), Teofilândia: (IBSP 57119); SERGIPE: Salgado: (MZUSP 7001, 7195–97, 7275–81, paratypes), São Cristóvão: (MNRJ 14057–58, MZUSP 11074).

Atractus punctiventris (*n* = 3).—**COLOMBIA:** META: Villavicencio: (MLS 254, holotype, MLS 102, MLS 255–56).

Atractus reticulatus (*n* = 34).—**ARGENTINA:** CORRIENTES: Galarza: Santo Tome: (UNNEC 7588), San

Miguel: (UNNEC 256–57), Formosa: Naicneck: Colonia Aborígine: (UNNEC 7219). **BRAZIL:** PARANÁ: Unknown locality: (MNRJ 9820), São José dos Pinhais: (MNRJ 9086); RIO GRANDE DO SUL: Candelária: (MNRJ 1261), Entre Rios do Sul: (CRUPF 309), Mato Castelhano: (CRUPF 991), Nicolau Vergueiro: (CRUPF 173, 176), Passo Fundo: (CRUPF 96, 199, 213, 224–26, 249, 284, 304, 309, 343, 376, 401, 416, 590, 686, 819, 829–30, 1064, 1204), São Lourenço do Sul: (NHM 1946.1.2.7, holotype); SÃO PAULO: São Paulo: (MNRJ 1524).

Atractus roulei (*n* = 2).—**ECUADOR:** AZUAY: Hierba Mala: (QCAZ 6256), Chimborazo: (USNM 33861).

Atractus cf. *taeniatus* (*n* = 7).—**BOLIVIA:** SANTA CRUZ: (MNKR not catalogued), Andrés Ibañes: Santa Cruz de La Sierra: Campus Universitario: (MNKR 17), El Vallecito: (MNKR 08, 3717), Km 8.5 Cochabamba-Santa Cruz de la Sierra road: (MNKR 321). **BRASIL:** MATO GROSSO: (MZUSP 2 specimens not catalogued).

Atractus taphorni (*n* = 5).—**VENEZUELA:** Unknown locality: (IBSP 25785); MÉRIDA: El Chorotal road to La Azulita: (CV-ULA 1838), La Carbonera: (CV-ULA 6417), Libertador: (ULABG 3909).

Atractus trilineatus (*n* = 16).—**BRASIL:** (IBSP 10126); RORAIMA: Boa Vista (MZUSP 9112), Taiano: Colônia Coronel Mota: (MPEG 479), Cachoeira do Cujubim: (MZUSP 6397–98, 6964, 7304–05), Ilha de Maracá: (MZUSP 9270), Mucajaí: (MZUSP 10473), Rio Jundiá tributary of Rio Catrimani: (MZUSP 6401, 6403), Santa Maria do Boiaco: (MZUSP 10328), Uarini: (MPEG 19015). **VENEZUELA:** MONAGAS: Río Guarapiches: (EBRG 2602); SUCRE: Sabaneta del Pilo: (MHNLS 13333).

Atractus ventrimaculatus (*n* = 11).—**VENEZUELA:** MÉRIDA: Betania: (ULABG 2409), La Princesa: (ULABG 6701–02), Libertador: El Valle: (MHNLS 897–901), Mérida: (NHM 1946. 1.5.15 holotype), La Mucuy: Parque Nacional Sierra Nevada: (MBUCV 2016), Pico Humbo: (EBRG 4052).

Atractus vittatus (*n* = 8).—**VENEZUELA:** ARAGUA: Unknown locality: (IBSP 41082), Colonia Tavor-El Limón road: (EBRG 700, 2959, 4059, 4092); DISTRITO CAPITAL: Caracas: (MBUCV 703), El Junquito-Colonia Tavor road: (MBUCV 415), El Limón: Las Aguaitas: (MHNLS 5159).